Ecological Modelling 379 (2018) 10–21

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Intermediate foraging large herbivores maintain semi-open habitats in wilderness landscape simulations

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ARTICLE INFO

Keywords:
Rewilding
Long-term vegetation dynamics
Natural mosaic landscape
Spatially explicit simulation

ABSTRACT

In the context of the rewilding Europe debate, the German national strategy on biodiversity aims to dedicate two percent of the German state area to wilderness development until 2020. Many of these potential large wilderness reserves harbor open habitats that require protection according to the Flora-Fauna-Habitat-directive of the European Union. As forests prevail in potential natural vegetation, research is required, to which extent wild large herbivores and natural disturbances may create semi-open landscape patterns in the long-term. We used the spatially explicit process-based model of pasture-woodland ecosystem dynamics WoodPaM, to analyze the long-term interactions between intermediate foraging large wild herbivores and vegetation dynamics in edaphically heterogeneous forest-grassland mosaic landscapes. We newly implemented a routine for intermediate foraging herbivores. We determined herbivore impact on vegetation from the quantitative balance between the demand and supply of herbaceous forage and woody browse. In abstract landscapes that represent the conditions in the established German wilderness area "Döberitzer Heide", we simulated potential future landscape dynamics on open land, in forest and along forest edges with and without intermediate foraging large herbivores and for a climate change scenario.

In our simulations the currently open landscape was conserved and even more the opening of current oak and beech forest was promoted. Canopy thinning and patch-mosaics of oak, birch, poplar and pine stands increased the overall nature conservation value in the long-term. To the contrary, open habitats were lost in simulations without herbivores. Moreover, our simulations suggested that intermediate foraging herbivores are especially suitable to maintain semi-open landscapes in wilderness areas, because (i) no additional winter forage was required, the natural availability of browse was sufficient. (ii) Their grazing maintained open land and their browsing thinned tree canopies even on poor sites that were unattractive for foraging. Here, habitat was maintained for threatened species from dry grasslands.

1. Introduction

As part of the rewilding Europe debate, the German national strategy on biodiversity (NBS; Jepson, 2016) aims to dedicate two percent of the German state area to wilderness development until 2020. In large nature reserves, all natural processes shall be protected in order to allow a course of vegetation succession that is free of anthropogenic influences, but driven by large herbivores and natural disturbances (Rosenthal et al., 2015; Jepson, 2016).

A minimum size of at least 1000 ha (500 ha in peatlands, river floodplains) and adjacent buffer zone shall guarantee a minimal impact of e.g. wildfire, windstorm and subsequent insect outbreaks to the surrounding landscape (refer to the bark beetle outbreak in the Bavarian Forest National Park, Heurich, 2001). This size will also allow a viable population of wild large herbivores to live from forage resources provided by the area itself.

Many of these potential German wilderness areas are currently far from a natural state, e.g. former surface mines or military training grounds, and harbor many habitats of open landscapes that require protection according to the Flora-Fauna-Habitat-directive of the European Union (FFH-directive). Without future human interference, a development towards closed forest is generally expected (Hofmann et al., 2008). Consequently, nature conservation has conflicting aims, wilderness on the one side (according to the NBS) and protection of endangered open habitats (according to FFH-aims) on the other side. The megaherbivore theory suggests a solution how this could be brought together. Re-introduced wild large herbivores could act as a natural "tool" to "maintain" semi-open wilderness landscapes without

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https://doi.org/10.1016/j.ecolmodel.2018.04.002
Received 13 July 2017; Received in revised form 27 March 2018; Accepted 2 April 2018
Available online 24 April 2018

direct human interference (in sensu *trophic rewilding* Svenning et al., 2016; Vera, 2009; Hodder et al., 2005).

Due to landscape cultivation since prehistoric times, large-scale natural wilderness and important large wild herbivore species are missing in Central Europe, such as wisent or wild horse. In turn, nature conservation faces a knowledge gap regarding the potential long-term development of future wilderness areas that host wild large herbivores (Hodder and Bullock, 2009; Cornelissen, 2017). Partial insights can be gained from large near-natural grazing systems on former military training grounds in Germany (Finck et al., 2009; Oheimb et al., 2006; Felinks et al., 2012; Anders et al., 2004; Lorenz et al., 2016) and from the rewilding project "Oostvaardersplassen" in the Netherlands (Cornelissen, 2017). However, in these systems the natural grazers (e.g. Heck-cattle and Konik horse) dominate the herbivore communities. Subsequently, deductions can mainly be drawn on the interactions among large herbivore grazing and vegetation succession. Similar experience is at hand on the influence of wild herbivore browsing on forest development (Kuijper et al., 2010b; Vandenberghe et al., 2008; Falinski, 1998; Falinski, 1998), but on the combined influence of grazing and browsing by intermediate foraging wild herbivores, such as wisent and red deer, a knowledge gap exists. Both species are promising for the open landscape conservation in German wilderness areas, regarding the recent experience in the "Döberitzer Heide" and the military training ground "Grafenwöhr" (Meißner et al., 2015). The body of research from the primeval Bialowieza forest (BNP, Samojlik and Kuijper, 2013; Miscicki, 2012; Kuijper et al., 2009) also provides indications. However, the knowledge transfer suffers from very distinct climatic conditions and a distinct forest composition, provision of supplementary forage during the long and cold winters, very low population densities when compared to the "Döberitzer Heide".

Moreover, the observations from near-natural grazing systems (Rosenthal et al., 2012) to the majority only provide short-term information (less than a decade) on how large herbivores influence landscape development. The experience in former military areas and in the rewilding project "Oostvaardersplassen" is of similar shortage in the light of processes of natural landscape dynamics that aim cover forest growth and decay and therefore centuries. In general, observations and experimental data focus on early successional pathways, such as tree seedling establishment under herbivore pressure facilitated by nurse shrub (Smit et al., 2007; Vandenberghe et al., 2009) or trampling damage on the grass sward (e.g. Peringer et al., 2017). Nevertheless, these short-term observations show similar tendencies. Grazing by large herbivores was capable setting off succession dynamics and thus preventing dense forest formation (Finck et al., 2002; Oheimb et al., 2006; Lorenz et al., 2016; Cornelissen, 2017). A shifting-mosaic cycle of open and forested ecosystems in the landscape was suggested (Olff et al., 1999). Regarding the landscape-scale impact of browsing, in the primeval forest BNP, it was observed that the wild large herbivore community which mainly comprises browsers (red deer, roe and fallow deer), triggered vegetation structures of diverse successional stages, induced shifts in tree species composition and for a short time contributed to openness in forest gaps (Kuijper et al., 2010a; Miscicki, 2012).

However, it is unclear if selective habitat use for grazing and browsing by intermediate foraging herbivores truly combine these effects on vegetation, because of their low density when compared to grazing systems, and because their impacts on vegetation succession influence each other. Under forest canopy thinned by browsing, the herb layer provides more forage for grazing, similar to traditional pasture-woodlands (so called "Hudewald", e.g. Kirby, 2004). On the one hand-side, low grazing pressure on grasslands allow shrub development, which provides browse forage outside forest. Such browse might be preferred by herbivores, because it is easy to access and the attractiveness of shrub species themselves (e.g. *Calluna vulgaris,* (Lorenz et al., 2016). It is therefore unclear, if intermediate foraging herbivores will keep grasslands clear from shrub and tree as grazers do in pasture-woodlands, and if they will thin forest canopy as browsers do in closed forest. These interactions are further complicated when considering edaphic heterogeneity in large nature reserves. Poor soils provide low-quality herbaceous forage and these sites are poorly grazed and turn into forest in the long-term. In pasture-woodlands, the forest-grassland mosaic patterns therefore strongly depend on the edaphic conditions (e.g. Lederbogen et al., 2004). On the other hand-side, the naturally thin-canopy forest on poor soil provides attractive browse.

Altogether, an integrative analysis is therefore required of grazing and browsing impacts on vegetation succession and long-term landscape patterns (especially maintenance of open habitats) in German wilderness areas, in which rewilding with intermediate foraging wild herbivores shall take place. Moreover, climate change impacts need to be considered because of the long-term development of woody species and because upcoming summer droughts may inhibit woody plant establishment on grasslands (Hopf, 2016), trigger shifts in tree species composition of forest (Hofmann et al., 2008). Climate change may therefore alter the future course of succession (Schulze et al., 2016). Several previous studies already addressed landscape development under herbivore pressure with special regard to the influence of large wild herbivores on forest development, open landscape conservation respectively (Jorritsma et al., 1999; Danell et al., 2006; Kramer et al., 2003; Weisberg et al., 2005). These studies either focused on browsing or were spatially implicit, and therefore disregarded the complexity of intermediate foraging in heterogeneous landscapes.

In our modelling study, we analyze the long-term interactions among grazing and browsing by intermediate foraging wild herbivores and herb layer and woody-plant vegetation dynamics using the wilderness area "Döberitzer Heide" as study site. We put the fundamental process-to-pattern relationships shown in Fig. 1 into the context of edaphic heterogeneity and climate change (Fernandez et al., 2017; Jeltsch et al., 1997). Central to our approach is the implementation of a quantitative food chain for herbivore grazing and browsing into the spatially explicit model of pasture-woodland ecosystem dynamics WoodPaM (Gillet, 2008; Peringer et al., 2013, 2015, 2016). Over long time scales, the balance between herbivores' forage demand and supply

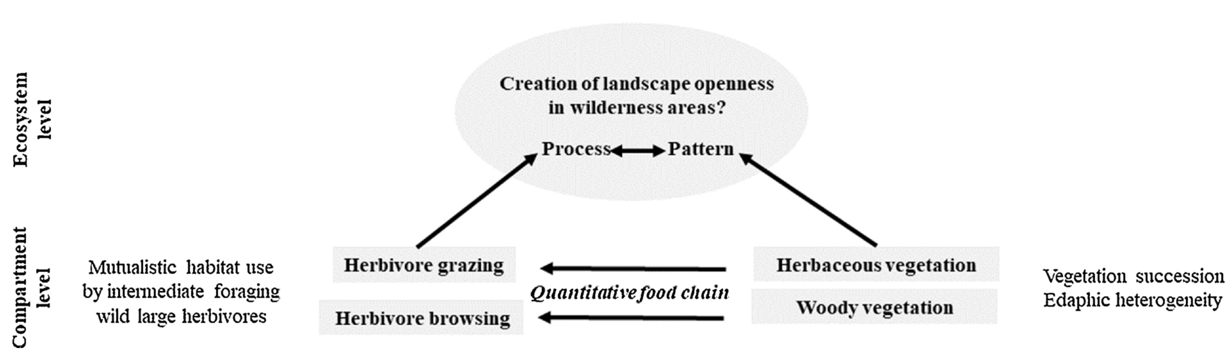

Fig. 1. Selected herbivore-vegetation interactions thought to be fundamental for mosaic landscape patterns implemented with our modelling approach.

from vegetation is fundamental for semi-open landscape development in wilderness areas. The mutualistic herbivore habitat use of combined browsing and grazing intensities control vegetation patterns (Vera, 2009; Fernandez et al., 2017). In comparison to previous studies (Jorritsma et al., 1999; Kramer et al., 2003; Weisberg et al., 2005), our model for the first time spatially explicitly analyses the effects of intermediate foraging wild large herbivores in heterogeneous landscapes and thereby links processes to mosaic patterns.

We explored the herbivore and climate change driven landscape dynamics starting from three artificial initial landscapes that represent characteristic elements of the real landscape mosaic. In order to separately analyze succession dynamics (regression, progression, and neighboring effects) in open (treeless) landscape, forest edge and forest in scenario simulations. We aim to find out:

Q1: Can intermediate foraging of wild large herbivores at low “natural” densities maintain and create semi-open landscapes as suggested by the megaherbivore theory?

Q2: How does selective habitat use for grazing and browsing of intermediate foraging wild large herbivores modify landscape patterns?

2. Material and methods

2.1. Study site

The “Döberitzer Heide” is a former military training ground in Northeastern Germany (N° 52.511528, E° 12.977092, Fig. 2) with gravelly-sandy substratum and subcontinental climate (annual mean temperature was 9.4 °C, mean annual precipitation was 582 mm in the reference period 1961–2014). Military use started in 1713. In 1990, the site was abandoned. Since 2004, it belongs to the Heinz Sielmann Stiftung, which declared 1.860 ha as wilderness area.

In 2010, common wild herbivores (red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, fallow deer *Dama dama*) were complemented with wisent (*Bison bonasus*) and wild horse (*Equus ferus przewalski*) in the fenced wilderness core area (the current numbers of individuals considered in this study are given in Table 1).

2.2. The WoodPaM model

WoodPaM is a grid-based model (square cell size is 25 m) that operates at a yearly time step. At the cell level, it simulates the dispersal, establishment and growth of tree species and shrubs and the succession

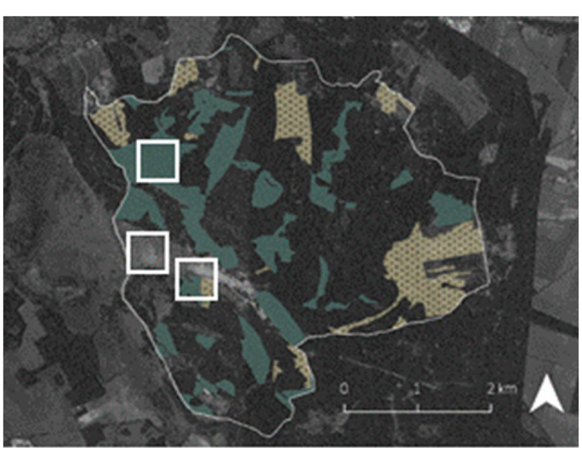

Fig. 2. Aerial image of the study site “Döberitzer Heide”. Outlined is the wilderness core area (1.860 ha) that represents a dynamic landscape mosaic of patches with e.g. mixed oak forest (blue) and dry heathland (dotted beige). White boxes define the abstract model landscapes that represent the three occurring states of open landscape, forest edge and forest. In reference to Giesbrecht (2017). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Table 1
Current herbivore community in the wilderness core area of the “Döberitzer Heide” (ca. 2000 ha).
Data source: J. Fürstenow, pers. comm.

Herbivore species	Number of herbivore individuals	Individuals/hectare
Wisent	90	0.05
Red deer	90	0.05
Wild horse	29	0.01
Density of the herbivore community:		0.1

of herb-layer communities. At the landscape level, it simulates the neighborhood dispersal and the long distance dispersal of tree species, as well as the selective habitat use of livestock. Habitat selectivity considers the availability of herbaceous forage and browse and tree cover. Thereby, a feedback is established in the model among the vegetation patterns at landscape-scale and the grazing and browsing impacts on woody plants and the herb-layer dynamics at the local-scale of grid cells (general framework in Peringer et al., 2013, 2015, 2017).

The baseline parameterization of herbivores’ habitat use reflected the preferences of cattle, which focuses on productive grasslands and disregards dense tree canopies for foraging (Kohler et al., 2006). For our study, we newly implemented the browsing behavior of wild intermediate herbivores. Our newly implemented browsing routine was inspired by the approach of Hudjetz et al. (2014), who considered the factors of mean plant woody biomass, mean body weight and seasonal forage consumption of red deer. Simulated browsing impact on tree species was determined by the balance among forage demand (kg dry woody matter of seedlings, twigs, bark) for each herbivore species and browse availability from tree species and shrub (kilograms dry matter of edible browse based on estimations (Kalén and Bergquist, 2004; Annighöfer et al., 2016; Kalén and Bergquist, 2004; Annighöfer et al., 2016). Browsing impact caused mortality of seedlings and reduces growth rates of saplings and shrubs based on the browsing tolerance index established in the LandClim forest model (Schumacher and Bugmann, 2006). Herbivores’ preferences for certain tree species were modelled based on observations by (Kuijper et al., 2010b), who established a selectivity index for browsing. We therefore simulated a selective browsing behavior, so that habitat use related to tree species and overall browse availability.

For adaptation of WoodPaM to the study site, we modified the submodels of tree, shrub and the herb layer. The Supplementary material provides a detailed description of our model modifications (Fig. 3).

2.3. Simulated landscapes

We performed simulations in a planar artificial model landscape of one km^2 size (40 × 40 grid cells). In this model landscape, heterogeneous edaphic conditions were represented by a central area of drought stressed shallow soils and surrounding deep soils (see Fig. 4). Moreover, a watering point was included, which attracts herbivores to the Southern landscape edge in order to compare landscape dynamics on attractive and remote sites of the wilderness area. However, the watering point had no effect on vegetation growth.

The simulated climate is based on a combination of observed climate from year 1901 to 2015 AD (data source: PIK and DWD) and of a reconstructed climate time series from year 1 to 1900 AD (Moberg et al., 2005) in monthly resolution for temperature and precipitation. We chose a moderate future climate change scenario with a temperature increase of 2.6 °C from 2011 to 2100 AD (rcp4.5, data source: PIK).

2.4. Design of simulations

In a two-step procedure, we first ran a spin-up simulation starting

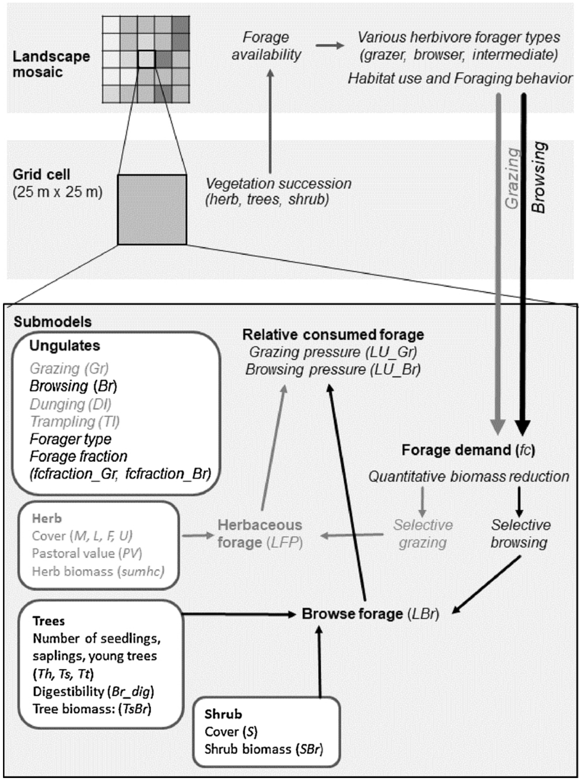

Fig. 3. Structure and main process interactions of the newly implemented routine for browsing by intermediate foraging large herbivores in the WoodPaM model. For the general framework of the WoodPaM model, refer to Peringer et al. (2013, 2015, 2017) and for a detailed description of the parameters refer to the Supplementary material.

from 10 seedlings of each tree species per grid cell towards the development of a mixed forest that approximates the current forest composition from 1850 to 1990 AD: a dense mixed oak-birch-poplar and beech-hornbeam forest with only a few forest glades (Fig. 5). The results demonstrate the realistic parameterization of tree species competition and were used to calibrate the newly implemented tree species parameters. The simulation ran along the climate time series and considered the mortality of old trees in terms of a yearly gap creation in 0.25% and shrub mortality in 2% of the landscape, number of cells respectively. These values relate to the maximum age of trees and shrub, from which decay the corresponding gaps emerge (refer to Chapter 2.7 in the Supplementary material).

From the vegetation data of this landscape (tree and herb layer), we created three distinct landscapes in order to initialize the model for scenario simulations in the second step (see Fig. 4). In each landscape, we simulated long-term vegetation development reaching from 1990 to 2300 AD for two scenarios: absence or presence of the current herds of intermediate herbivores (Table 1) for 365 days per year from 2010 AD onwards. We numbered the landscape scenarios according to their initial landscape state at topmost-level: the open landscape scenarios belong to the scenario family “1”, forest edge “2” and forest “3”. At sub-level, the numbering indicated which scenario type was simulated: the absence of large herbivores “1” or the presence of large herbivores “2”.

The simulated herds sum up to a density of 0.1 individuals/hectare with an intermediate forage demand comprising 67% herbaceous (forbs, grasses, fruits) and 33% woody (twigs, seedlings, saplings) forage matter (ca 14.8 daily forage consumption kg/individual). We lacked long-term data on herbivore population dynamics, and to avoid uncertain variability in simulations, we therefore simulated the status quo density. For details on the estimate of stock density and diet composition, refer to the Supplementary material.

2.5. Model plausibility testing

The tree species competition and sequence of successional stages was subject to calibration in the spin-up simulations. The climate sensitivity of tree species was tested for historical climate fluctuations in (Schulze et al., 2016) and led to plausible results.

The herbivore impact on vegetation development builds on our bottom-up approach that balances foraging demand and available herbal and woody forage in terms of biomass (kilogram dry matter) based on observed data. The general framework of herbivore behavior at landscape scale was tested many times in previous studies in pasture-woodlands (Peringer et al., 2013, 2015, 2016).

2.6. Landscape analysis

For the analysis of landscape structures, we recorded habitat diversity and spatial distribution of habitats at landscape scale along all scenario simulations. The habitat types were defined following (Gallandat et al., 1995) according to tree cover (Table 2). In order to explain habitat formation and quality mechanistically, we also recorded the distribution of tree species, the cover of herb layer communities and the habitat use of herbivores in terms of residence time per grid cell.

3. Results

The temporal development of landscape structures and corresponding habitat diversity differed strongly between all scenario simulations, i.e. for initial landscape states (open landscape, forest edge, and forest) and for the presence of herbivores. In the following, we characterize major aspects in landscape dynamics that correspond to our research questions.

3.1. Conservation of open landscape

In the **open landscape scenario** and the **forest edge scenario without herbivores** (Scenarios 1.1 and 2.1), progressive succession towards forest occurred within one century (Fig. 6). Successional trajectories on open landscape showed fluctuating lines of habitat types that indicate the fast replacement of treeless grassland and thin canopy, early successional woods by forest within a few decades. These shifts

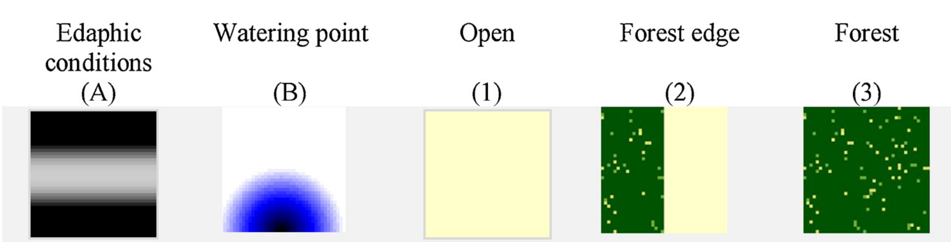

Fig. 4. Model landscape and initial landscape patterns at simulation start. From left to right: (A) and (B) the gradually changing heterogeneous edaphic conditions in the model landscape. (A) White area represents drought stressed shallow soils that are contrasted to deep soils in black. (B) In the Southern landscape area there is watering point, the attraction for large herbivores decreases with increased distance to its center (dark blue). The initial states of landscape patterns and their scenario family numbers: (1) open (treeless) landscape, (2) forest edge with one-half forest and other half-treeless and (3) closed forest. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

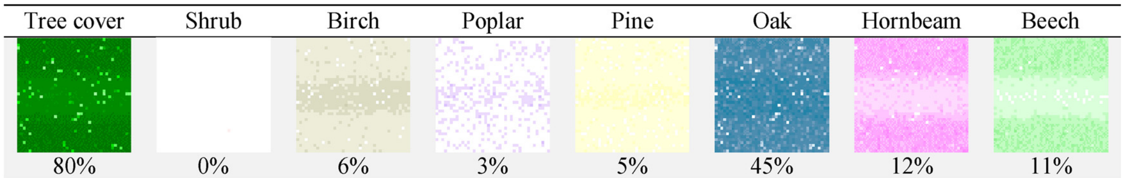

Fig. 5. Landscape state and forest community in 1990 AD from the spin-up simulation. Due to the crown overlap of trees, the sum of tree cover is not equal to total tree cover.

Table 2
Structural definition of habitat types for the analysis of simulation results (adapted from the phytosociological analysis by Gallandat et al. (1995)). The habitat types 1 and 2 provide habitat requirements for light-demanding herbaceous plant communities of open habitats (e.g. productive and poor grasslands) and dwarf shrubs.

Habitat class	Structural definition
1	Unwooded habitat with tree cover ranging from 0 to 2%.
2	Sparsely wooded habitat with tree cover ranging between 2% and 20%, trees or bushes being mostly scattered.
3	Medium wooded habitat with tree cover ranging between 20% and 50%, trees or bushes being scattered or clustered in thickets.
4	Densely wooded habitat with tree cover ranging between 50% and 70%, with trees mostly clustered in thickets.
5	Forest with tree cover higher than 70%, appearing as forest with a closed canopy.

among habitat types did not occur uniformly across the landscape, but in a mosaic of successional stages (the temporary decrease of the landscape structural diversity AIL in Fig. 6 indicates structurally diverse mosaics). However, the general trend towards densely wooded habitats is uniform.

To the contrary in **open landscape** and **forest edge scenarios with herbivores**, progressive succession was slowed for almost a century (densely wooded habitats emerged around 2050 AD in Scenario 1.1, but around 2150 AD in Scenario 1.2, Fig. 6). In the **forest edge scenario with herbivores** (Scenario 2.2), the cover of sparsely wooded habitats remained consistent in the very long-term. In the **open landscape with herbivores** (Scenario 1.2), progressive succession was only partly inhibited. Sparsely wooded habitats accounted for the major part of landscape structure and dominated around the watering point in the Southern landscape part (Fig. 7). In the remote Northern part, a mosaic of sparsely and densely wooded habitats emerged and increase landscape structural diversity (decrease of the AIL in Fig. 6).

3.2. Regressive succession in forest

In all **scenarios without herbivores**, closed forest persisted where initially present (Figs. 6 and 7, Scenarios 2.1 and 3.1). Climate change drove a tree species shift from beech-hornbeam-oak to oak-pine forest (Figs. 10 and 11). However, thin canopy forest in a mosaic pattern emerged only temporarily (decrease of the AIL and increase of densely wooded habitat, Scenarios 1.1, 2.1 and 3.1, in Fig. 6).

In the **forest and forest edge scenarios**, **herbivores** triggered regressive succession by thinning out of tree cover of forest towards densely wooded habitats with 50 to 70% tree cover (Scenarios 2.2 and

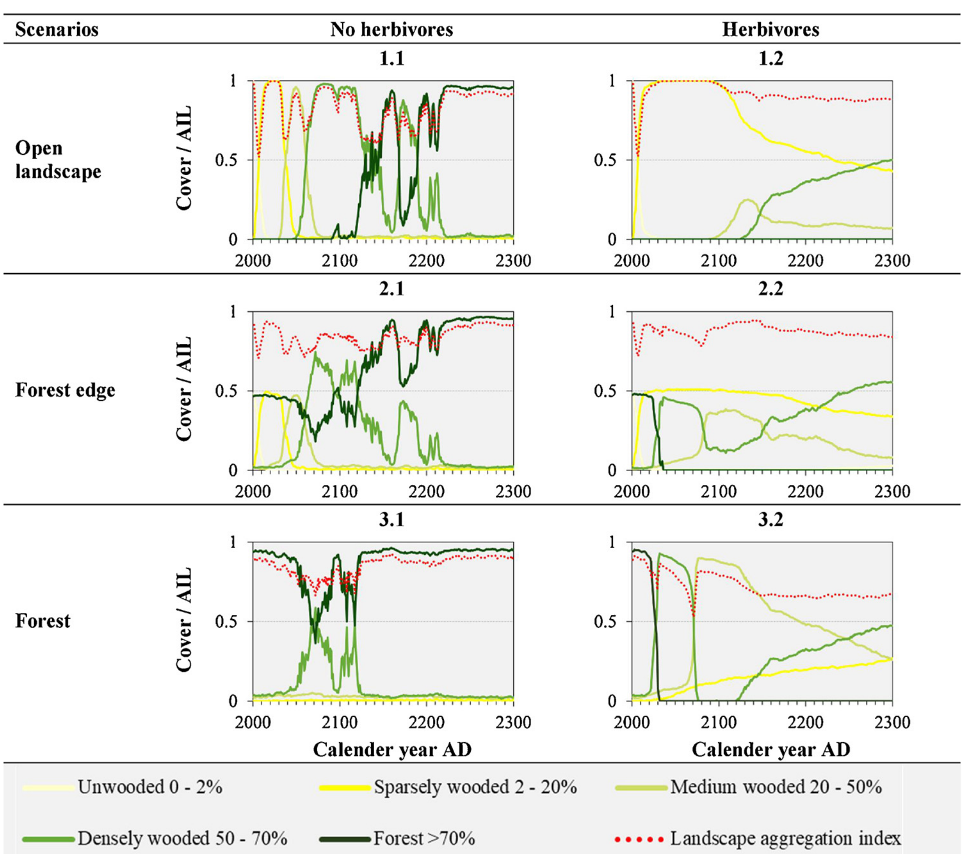

Fig. 6. Landscape dynamics: Trajectory lines represent relative cover of habitat types and landscape structural diversity (AIL, red dashed line). Lastly, values of the AIL towards zero indicate landscape heterogeneity and towards one indicate landscape homogeneity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

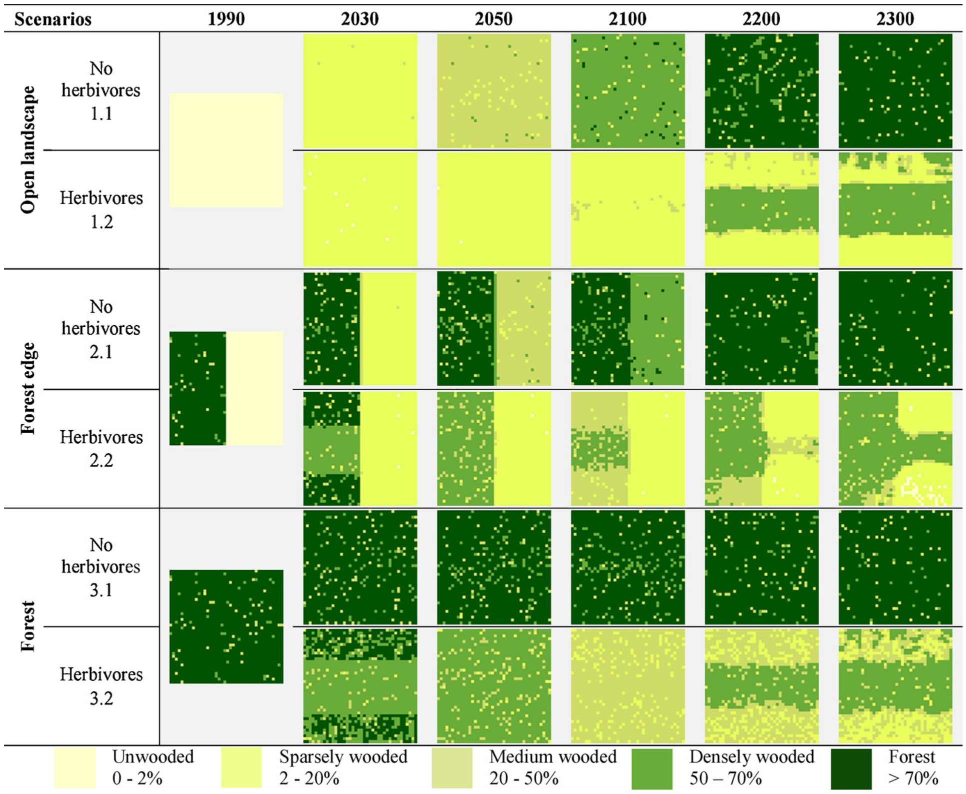

Fig. 7. Landscape-structural dynamics and spatial distribution of habitat types in calendar years AD.

3.2, Fig. 7). In the forest scenario, herbivores developed a structurally rich mosaic of sparsely, medium wooded and densely wooded habitats from initially homogeneous closed forest (Scenario 3.2, Fig. 6). In the forest edge scenario, herbivores selectively opened forest to medium wooded habitats close to the watering point in Southern part of the landscape, but failed to do so in the remote Northern part (Scenario 2.2, Fig. 6). In all herbivore scenarios, light demanding tree species (poplar, birch. pine) enriched tree species diversity of the forest stands on the cost of today present beech and hornbeam (Figs. 9–11). Oak persisted in all scenarios where initially present.

3.3. The role of an edaphic mosaic landscape

The **habitat use of herbivores for grazing** (Fig. 8) was strongly determined by edaphic conditions (Fig. 4). High grazing intensities (Fig. 8) occurred on deep soils with productive grasslands (Fig. A-1 in the Supplementary material), and in sparsely to medium wooded habitats (compare Figs. 7 and 8). In the **open landscape and the forest edge scenario**, the poor grasslands on shallow soils were disregarded for grazing (Scenarios 1.2 and 2.2 in Fig. 8). Woody plant succession was the consequence (Fig. 7).

In the forest and in the open landscape scenarios, the **habitat use for browsing** was more distinctly distributed according to edaphic conditions (Scenarios 1.2 and 3.2 in Fig. 8). In the **forest scenario**, the understory on rich soil was preferred to poor soil. In the **open landscape scenario** (and later on after canopy thinning in the forest scenario), patches of early successional tree species and shrubs were preferred (Fig. 9). In the open landscape scenario, even the poor soils partly became attractive for browsing because of their density of attractive tree species.

4. Discussion

Our scenario simulations of long-term wilderness development suggest that herds of intermediate foraging wild large herbivores may maintain semi-open landscapes in subcontinental heathlands and oak forests when moderate climate change is considered for the future.

In the following, we first discuss the accuracy of our modelling of specific processes and patterns of intermediate foraging of wild herbivores, and then the realism of our simulation outcomes in relation to the research questions. The model validation regarding reproduction of current tree species composition and outpost-tree colonization patterns on open landscape is discussed in Chapter 3 in the Supplementary material.

4.1. The accuracy of simulated intermediate foraging behavior

Weisberg et al., (2006) argue that the representation of herbivore-vegetation interactions requires the integration of multiple ecosystem compartments, most importantly vegetation and herbivores, in a balanced manner regarding their properties (tree, shrub and herb layer; foraging type of herbivores), processes (plant growth, herbivore behavior and habitat use) and the consideration of spatial heterogeneity and temporal dynamics. Otherwise, the goal of integrative ecosystem analysis cannot be reached. Our modifications of the WoodPaM model aimed to establish such a balanced model formulation for wilderness development, with special regard to the combination of grazing and browsing by intermediate foraging wild herbivores. WoodPaM was already successfully used to analyze herbivore-vegetation-climate interactions in cattle-grazed pasture-woodlands in the Swiss Jura Mountains (Peringer et al., 2013, 2015, 2016). Accordingly, our modelling of browsing by intermediate foraging wild herbivores was strongly oriented on the existing process formulations for grazing behavior of cattle and established a second pathway of forage consumption and impact on vegetation that was parallel and symmetric to grazing. Therefore, our browsing routines that were inspired by the approach of Hudjetz et al. (2014) fitted well into the existing model framework regarding a balanced level of mathematical detail (quantitative

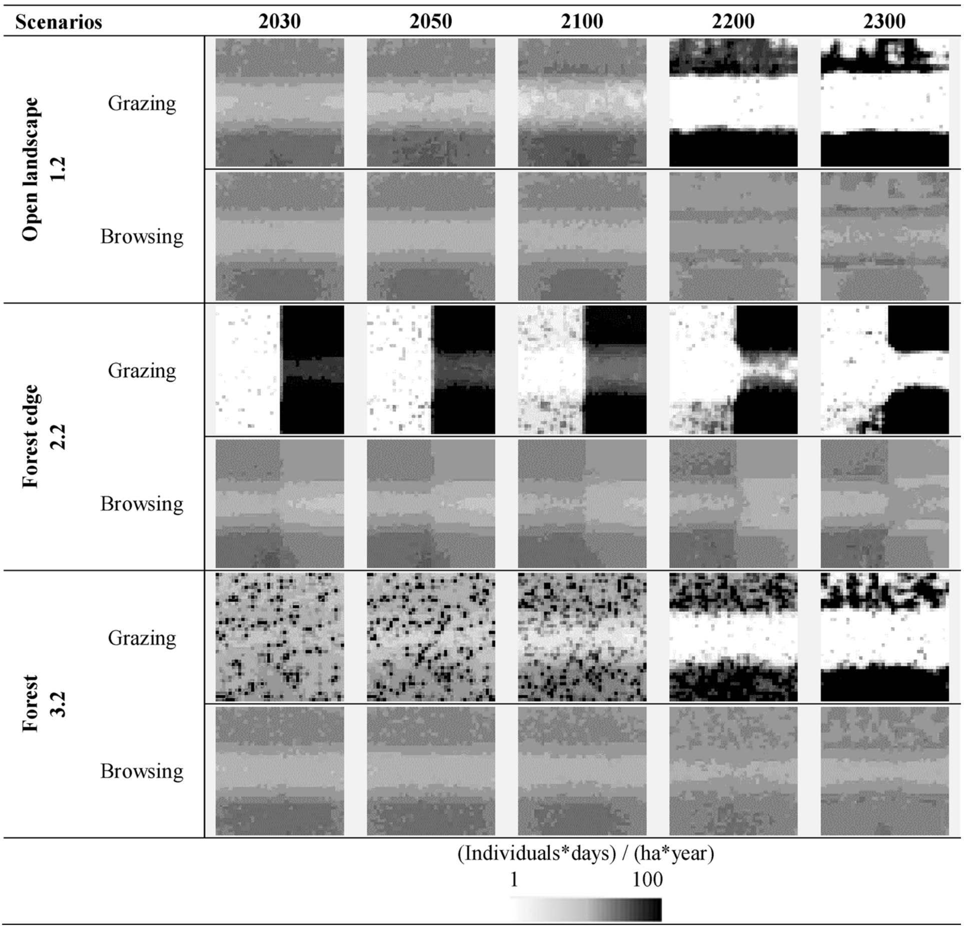

Fig. 8. Shifting habitat use of intermediate herbivores in the dynamic model landscapes corresponding to Fig. 7. Habitat use describes the mean residence time of large herbivore grazing or browsing activity per grid cell in a year. Darker tones indicate that the residence time of large herbivores in these grid cells was frequent and therefore foraging activity was intensive in the specific year. See Supplementary material Fig. A-2 for the corresponding consumption rates of herbaceous and browse forage at landscape scale.

estimate of food chain, refer to Chapter 2.1 in the Supplementary material) and their interaction with vegetation was plausible.

For wild large herbivores, the landscape-scale balance among the demand for and the availability of forage is central to survive and also an important determinant for the openness and tree species composition of wilderness areas (Jorritsma et al., 1999). Based on our quantitative estimate of the food chain regarding grazing and (newly established browsing following Hudjetz et al., 2014, Fig. 1), we could verify our modelling regarding the fact that during the past years, herbivore effects were observed almost everywhere in our study area, but plenty of forage remained by the end of the year (P. Nitschke, pers. comm.). The simulated utilization rates of browse reached about 50% and of course never exceeded browse supply (Fig. A-2, Supplementary material). Fundamental to this realistic balance among forage demand and supply was our explicit modelling of herbivores' diet and tree seedlings' proportion of edible biomass in terms of kilograms dry matter of woody browse. Furthermore, we therefore successfully modelled the two main factors for browsing habitat use, which are the availability of woody browse and its digestibility (Kalén and Bergquist, 2004). The simulated pattern of herbivore habitat use showed higher browsing activity in the forest area due to higher abundance of seedlings and saplings when compared to a treeless open landscape. However, browsing was also strong in the open landscape area, when pioneer tree species had established and provided browse of high digestibility (poplar, birch). Finally, the simulated browsing selectivity for certain tree species (basically the preference birch and hornbeam) realistically shifted tree species composition and distribution under herbivore pressure (Kuijper et al., 2009). In forest scenarios, the cover of hornbeam decreased because it is the most preferred among all tree species (Kuijper et al., 2010a). In open landscape scenarios, herbivore browsing reduced the cover of pioneer species (birch, poplar, pine) for centuries (Scenarios 1.1 and 1.2 until 2200 AD, Lorenz et al., 2016). Our model did not simulate nursery effects by shrubs for tree species establishment (Vandenberghe et al., 2009; Smit et al., 2007; Vera, 2000), we dedicate this to the low browsing pressure in our wilderness area when compared to low-intensity grazing systems.

A limitation of our simulation results is our disregard of herbivore population dynamics. Fluctuations in herbivore densities correlate with fluctuations of tree species in forest community and density shifts are known to have strong impact on landscape structure (Kuijper et al., 2009; Marris, 2009; Cornelissen, 2017). However, we lacked long-term data about the coupled population dynamics of wisent and horse under the conditions of the study area and when in competition for grazing resources. Further, no data was available about population dynamics under natural conditions without human interferences of supplementary feeding or population regulation. A population increase may have unexpected effects, on herbivore-interspecific competition as observed in the grazer dominated rewilding project "Oostvaardersplassen" (Cornelissen, 2017). Further, a fivefold decrease of browsing pressure by red and roe deer affected tree regeneration of deciduous tree species positively in the short-term, and in the long-term influenced the loss of open habitats (Kuiters and Slim, 2002). We therefore preferred to simulate the status quo herbivore densities, for which the carrying capacity of the study area is sufficient, instead of the introduction of uncertain variability in our simulations.

4.2. Maintenance of semi-open landscape by intermediate foraging large wild herbivores

Our scenario simulations suggested the potential of intermediate foraging herbivores at "natural" low densities to maintain and create semi-open landscapes. This simulated effect on open landscape

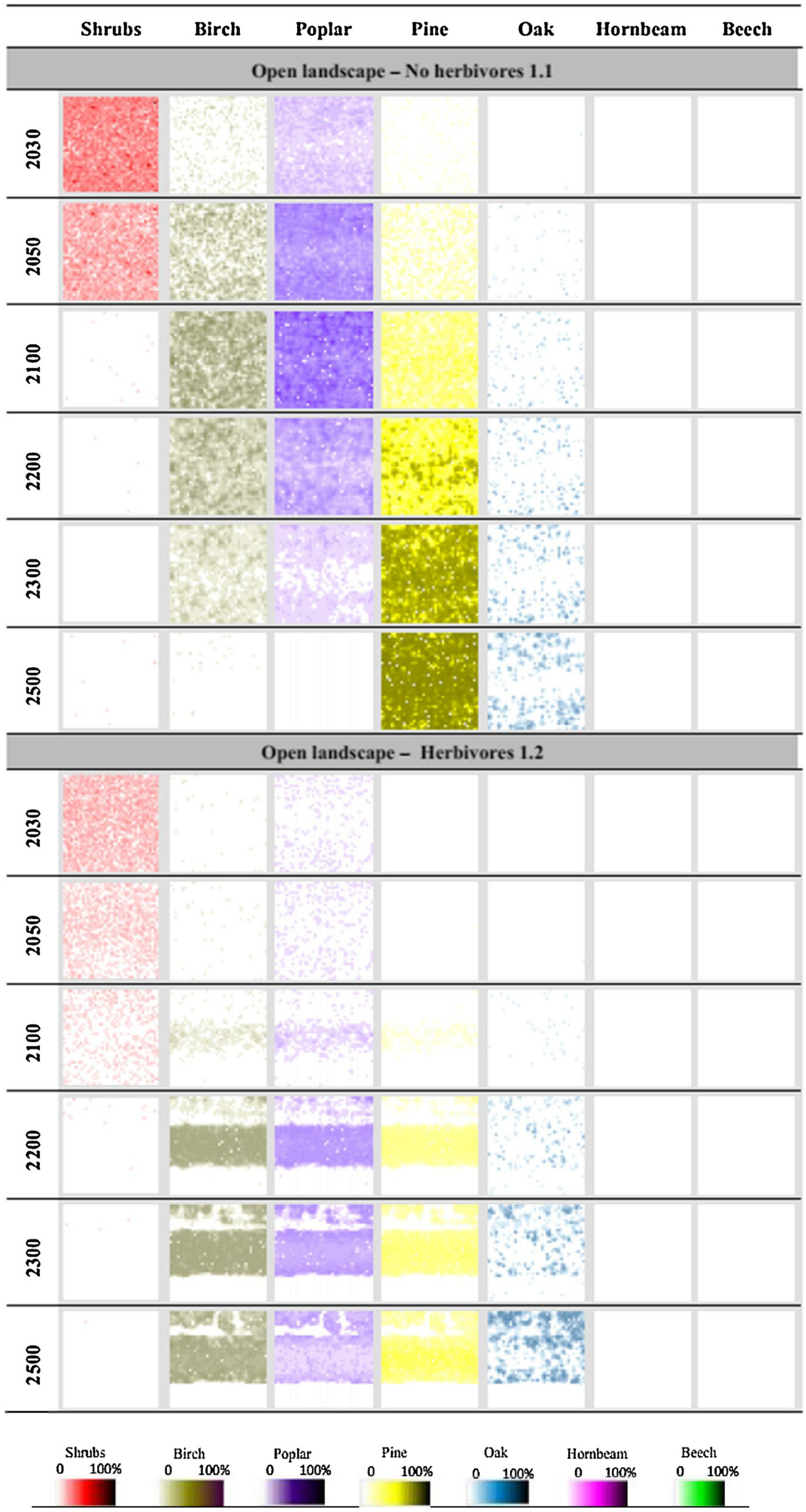

Fig. 9. Distributions and cover of woody species in the scenarios without herbivores (top) and with herbivores (bottom) in the open landscape scenario.

conservation was reliable because it built on our modelling of the quantitative food chain regarding the combination of grazing and browsing, which is specific for intermediate herbivores (Chapter 4.1). A semi-open mosaic landscape was achieved similar to applications of low-intensity grazing systems by nature conservation (Cornelissen, 2017; Lorenz et al., 2016; Finck et al., 2009) although the density of intermediate herbivores was much lower than of grazers. We dedicate this simulated efficiency of intermediate herbivores to their combined impact on both the herbaceous vegetation by grazing and the tree and shrub vegetation by browsing (Vera et al., 2006) and to the impact of climate change. Similar low densities of browser dominated herbivore communities (red, roe and fallow deer) did not maintain forest gaps (Samojlik and Kuijper, 2013). We consider future climate induced drought stress on tree species regeneration to play a crucial role,

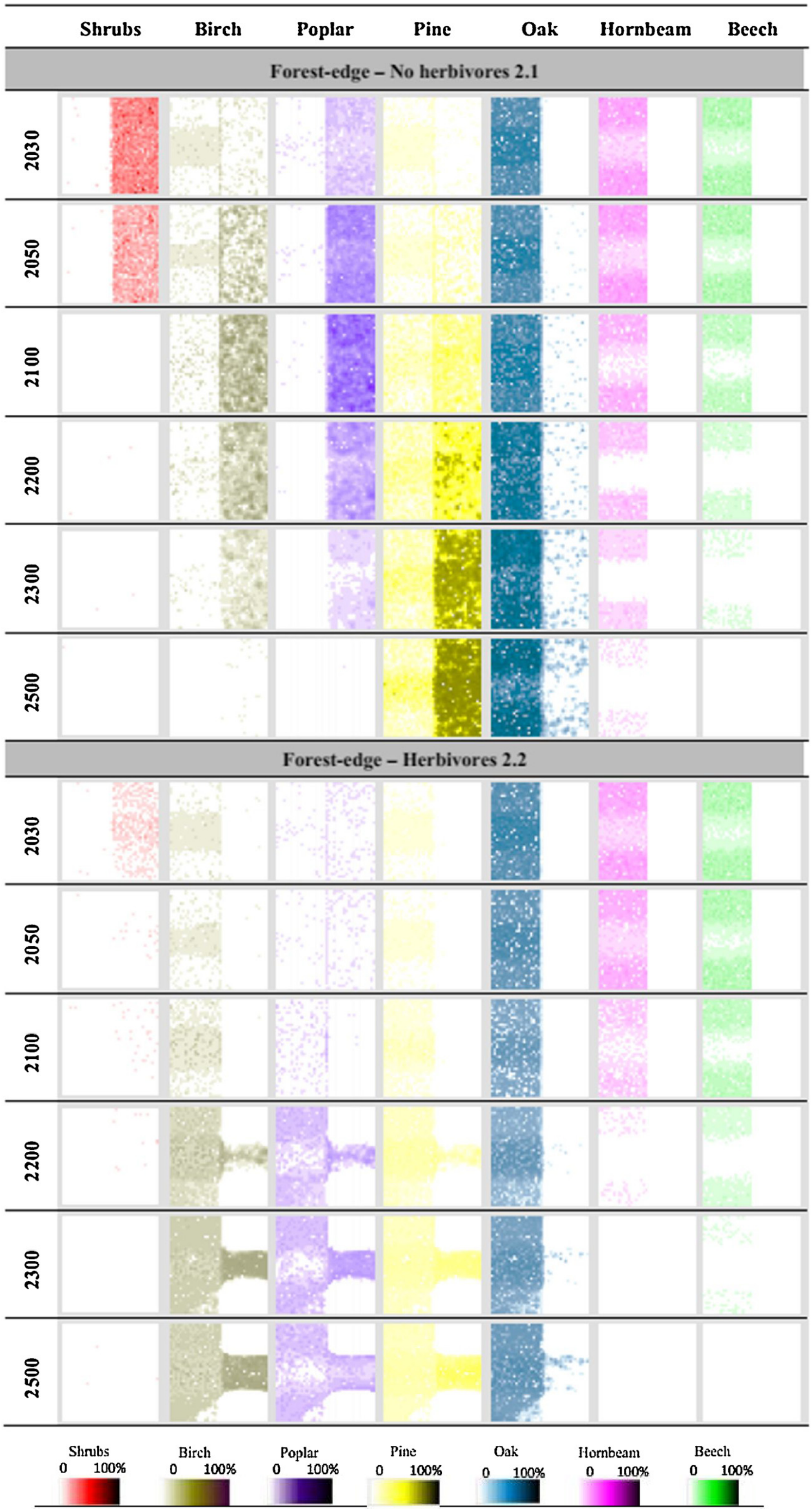

Fig. 10. Distributions and cover of woody species in the scenarios without herbivores (top) and with herbivores (bottom) in the forest edge scenario.

because recent observations indicate that summer droughts restrict the establishment of pioneer tree species in the open landscape (refer to the high mortality of birch in the experiments of Hopf, 2016). Historical observations might not provide a basis for the future landscape dynamics (Schulze et al., 2016). With our integrative analysis of herbivore-vegetation interactions in the light of climate change, we complement the analysis of historic landscape dynamics and gained new insights on the potential of intermediate herbivores for open landscape conservation in wilderness areas. Our results support that (intermediate) large herbivores are indispensable for the maintenance of landscape mosaics of grassland-, shrub and forest habitats (Bakker et al., 2016, Vera, 2000).

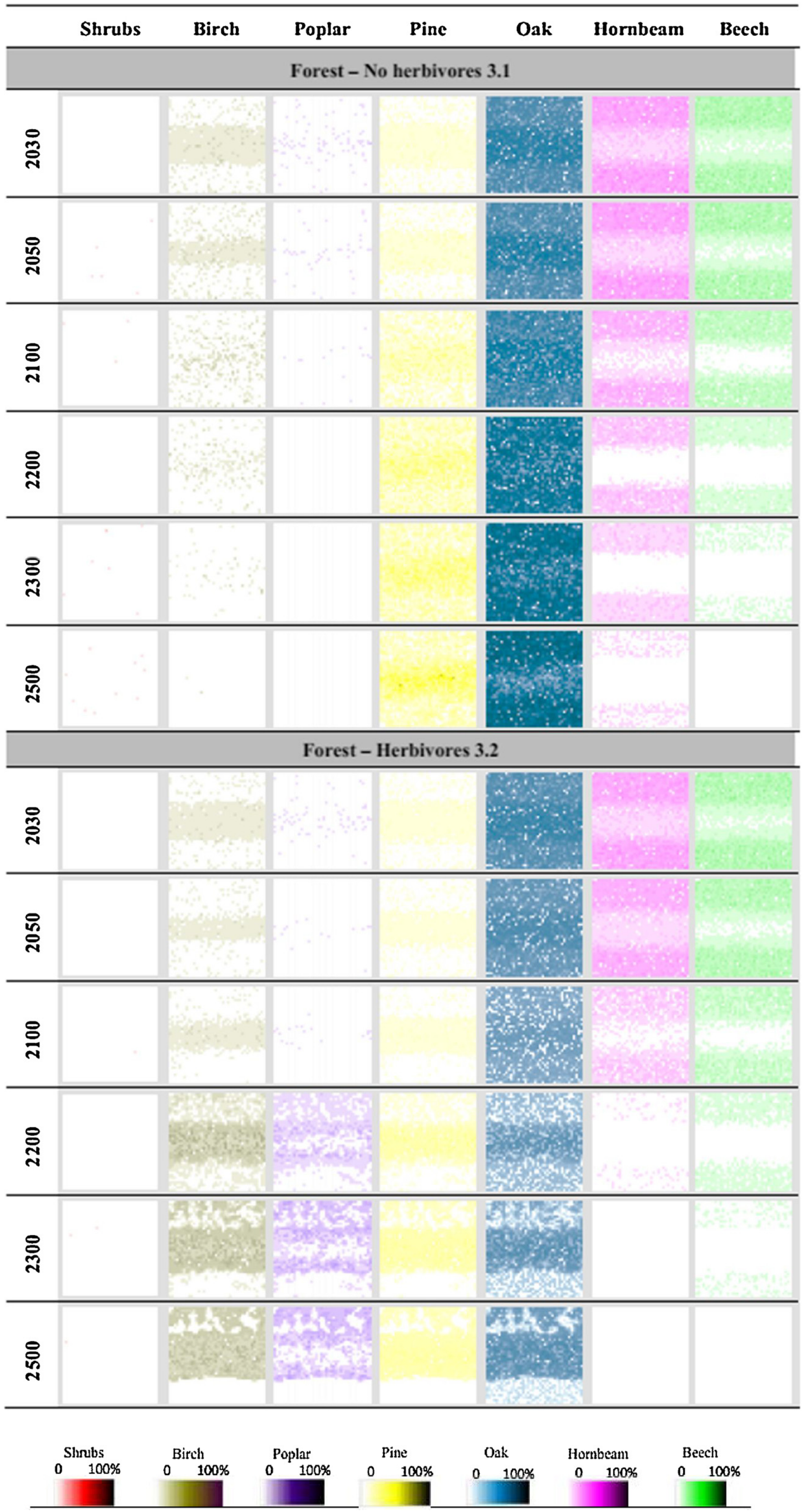

Fig. 11. Distributions and cover of woody species in the scenarios without herbivores (top) and with herbivores (bottom) in the forest scenario.

4.3. Modification of landscape patterns by selective habitat use of intermediate foraging wild large herbivores

Similar to observations in low-intensity pasture-woodlands that were dominated by grazers, the grassland-forest-mosaics that were created by intermediate foraging wild herbivores in our simulations showed the segregation of grasslands on main foraging sites from woods on poor soils with unattractive forest. Such forest-grassland segregation is generally evaluated negative from the nature conservation perspective, because forest development leads to habitat loss for threatened species that depend on e.g. dry grasslands. As shown in the case of lime stone ridges in the pasture-woodlands of the Swiss Jura

mountains, Dufour et al., 2006), on grazed oligotrophic fens (the case of Northern pre-alpine pasture-woodlands, Lederbogen et al. (2004), and in our simulation the habitat quality for threatened species of dry grassland habitats (e.g. FFH-code 4030, FFH-code 9190, Dipner, 2005).

However, in contrast to the grazer-dominated systems, the woods on poor soil did not develop towards dense forest but towards thin canopy forest. In turn, a high nature conservation value (Dipner, 2005) was maintained on these sites, because of their richness in tree species diversity and indicated habitat for grassland species in the understory. This development depended on the natural browsing demand of intermediate foraging herbivores, which, in contrast to grazers, browsed the unattractive forage sites, where pioneer tree species provided attractive forage (birch, poplar). The simulated effects of mutualistic habitat use support the hypotheses that in the past, multispecies´ communities of large herbivores triggered successional pathways towards a decrease of woody cover and increase in light-demanding species (Vera, 2000, Bakker et al., 2016). Our simulations thereby demonstrated that intermediate foraging large herbivores have the potential to evoke species-rich semi-open habitats on drought prone shallow soils that are otherwise disregarded by grazers and habitats are lost.

4.4. Conclusions for nature conservation

Our simulations suggested the capability of intermediate foraging wild large herbivores to play a crucial role for open landscape conservation in wilderness reserves even at low densities. Their mutualistic habitat use covered the entire landscape and showed positive effects in both open habitats and forest regarding nature conservation value. Thus, they do not require additional winter forage.

Open habitats were partly conserved by herbivores (dry heathlands) and secondary forest as well as today's forest were enriched in tree species diversity (mixed stands with birch and poplar instead of pure pine stands). Even on sites with unattractive forage (dry grasslands on shallow soil), browsing thinned out forest canopy towards the development of a steppe heath structure.

Regardless regressive succession, today's forest showed a strong *legacy effect* regarding spatial distribution and dominant species, which is of specific importance for the habitat continuity for the rich biodiversity of oak stands.

Considering these positive effects, we therefore argue to integrate large herbivore communities with distinct foraging strategies in wilderness development in order to enhance the nature conservation value of these reserves.

Acknowledgements

We thank Peter Nitschke and Jörg Fürstenow from the Sielmann Stiftung GmbH for supportive information and data, and Eugen Giesbrecht for support in graphic implementations. We thank Uwe Riecken from the German Federal Agency for Nature Conservation (BfN) for constructive discussion of results, and for support by the BfN as part of the Research & Development project WildesOffenland (FKZ 3515850500).

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ecolmodel.2018.04.002.

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